DISTRIBUTION OF EPIPHYTES IN A RUBBER PLANTATION IN SARAWAK

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Epiphytic plants exhibit complex patterns of distribution. A given species is usually geographically confined to a particular climatic zone and type of forest, and within the forest favors certain microhabitats. The local distribution depends on the species of host trees, their position, age and condition, and on the presence or absence of other epiphytes. These factors interact in complex ways that make it difficult to interpret phytosociological data and local patterns of distribution, though several attempts have been made to do so in Java (Went, 1940), Micronesia (Hosokawa, 1943) and West Africa (Johansson, 1974).

A uniform stand of trees, such as may be found in cacao or rubber plantations, offers certain advantages in the study of the distribution of epiphytes. Only a single species of host tree is present, the trees are of uniform age and size, and usually are regularly spaced in a rectangular grid. Thus several variables affecting the distribution of epiphytes are controlled. This paper reports observations on the distribution of vascular epiphytes in a plantation of rubber trees [*Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg.]

When a rubber plantation is planted, the forest is clearcut and burned and young trees from a nursery are set out in rows. At the time they are planted, there are no epiphytes in the trees. As the plantation matures individual trees are colonized by epiphytes; the seeds of the colonizing species arrive from epiphyte populations in nearby primary forest or from neighboring older plantations.

Two aspects of the distribution of epiphytes were investigated in this study: the distribution of individuals of a species, and the distribution of one species of epiphyte with respect to another. The first of these is predominantly concerned with patterns of seed dispersal and colonization, and the second emphasizes the biological interaction of epiphytes with each other.

Several simple models of seed dispersal may be relevant to the colonization of a rubber plantation. For an epiphyte with wind-dispersed diaspores (anemochory), the density of the seed rain will diminish geometrically with distance from a source. This distribution is described by a family of hyperbolic curves the steepness of which reflects the weight and aerodynamics of the seeds. Within a new rubber plantation distances from epiphyte seed sources are great enough that the seed rain is of low density. With a number of seed sources surrounding the plantation, there will be an essentially uniform seed rain resulting in a random distribution of colonizations by a particular epiphyte species.

Once an anemochorous epiphyte is established in the plantation and reaches maturity, then it is most likely to colonize adjacent trees, and a contagious distribution of the species should result with a cluster of progeny established close to the parent plant.

Fleshy-fruited species with seeds carried internally by animal dispersers (endozoochory) may be expected to have a different distribution from anemochorous species in the case of dispersal from a point source. It is more

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likely that the dispersal vector will deposit the seeds at a distance from the source than in or adjacent to the source tree itself, especially since the epiphytes in question present scanty fruit crops which do not encourage prolonged feeding in one spot. However, beyond a certain distance the normal range of the vector is exceeded and density of seed rain again diminishes.

For the size of plot here mapped (approximately 1 hectare) even secondary dissemination from an epiphyte established in the plantation probably would not show contagious distribution for bird-dispersed species. This reflects that the size of quadrats and scale of the study are critical in determining random and non-random distribution of plant species.

Where several species of epiphytes occur together they may be distributed independently of each other, or they may be positively associated (gregarious), or negatively associated. These associations can reflect parallel responses of several species of epiphytes to relevant aspects of the environment, or interactions of the epiphyte species with each other. The association of two species (random or gregarious) may be independent of the individual patterns of distribution of each of the species (random, contagious, or hyperdispersed).

METHODS

The study site is within a rubber plantation located at km 24 from Kuching on the road to Bukit Krian, Sarawak, Malaysia (N. Borneo). The landscape is one of low rolling hills at an elevation of 50-200 m. Before being cleared for agriculture, the region was covered with tropical rain forest. The plot mapped was within a large plantation on fairly flat ground; the plantation was surrounded by a strip of second-growth forest beyond which were additional rubber plantations of a similar age. These represent an area of land that was cleared after World War II. The nearest patches of remaining primary forest are more than 0.5 km distant.

The rubber plantation is composed of parallel rows of trees about 8 m apart, and within each row the trees are planted 2.5-3 m apart. The branches of adjacent trees within a row were strongly interpenetrating, but the branches of trees in adjacent rows hardly touched. The rubber trees were 20-40 cm DBH and 8-12 m tall.

The distribution of vascular epiphytes in a plot ten rows wide and twenty trees deep was mapped. The plot was located within the plantation to avoid edge effects. Because it was the dry season (February), the trees were mostly without leaves, facilitating the observation of epiphytes. Mapping was by ground observation using binoculars and by tree climbing. Because many of the epiphyte species have creeping habits or various means of vegetative reproduction, it was not considered feasible to estimate the number of epiphytic individuals per tree; instead only presence or absence of the epiphyte species was scored.

Association between pairs of epiphyte species was determined using a chi-square test. The association tested was simply the occurrence of the two epiphytes in the same tree, whether or not they were in actual contact.

Randomness of distribution of particular species was tested by dividing the sample area into quadrats consisting of five adjacent trees in a row. A chi-square goodness-of-fit test was then used on the observed frequencies of trees occupied per quadrat compared to a Poisson distribution. This test would somewhat underestimate non-random distribution since it does not

account for occurrence of the epiphytes in adjacent trees which happen to be in different quadrats, or in adjacent rows.

Independence of colonization of trees by different epiphyte species (vs. gregarious distribution) was tested by a chi-square goodness-of-fit test of the observed frequencies of trees with a given number of epiphyte species to frequencies expected for independent colonization as indicated by a Poisson distribution. This test includes the assumption that the occurrence of an epiphyte species in a tree represents a single colonization event. This assumption is not unreasonable for the sample in question, given the low density and abundance of the epiphytes and young age of the plantation.

RESULTS

The distribution of epiphytes in the plantation is shown in Figure 1. Twenty-five species of vascular epiphytes were present in the plot, (9 species of orchids, 6 species of fern, 6 species of asclepiads, and 4 species of berry-fruited dicotyledons).

Each of the fern and orchid species (except one *Dendrobium*) were randomly distributed in the plantation. Of the fleshy-fruited epiphytes three were randomly distributed; a fourth (*Myrmecodia tuberosa* Jack) showed a significantly contagious distribution ($p<.01$). The species of epiphytic Asclepiadaceae showed a highly clumped distribution ($p< .001$ for *Dischidia collyris* Wall., $p<.01$ for *D. rafflesiana* Wall. and *D. gaudichaudii* Decne.). These species not only tended to occupy adjacent trees in a row, but also occupied neighboring trees in adjacent rows.

Not only were the individual species of Asclepiadaceae contagiously distributed, but they also were gregarious with other epiphytic Asclepiadaceae. A chi-square test shows a significant association of *Dischidia collyris* and *D. rafflesiana* ($p<.001$), *D. collyris* and *D. gaudichaudii* ($p<.001$), and *D. rafflesiana* and *D. gaudichaudii* ($p<.01$). *Dischidia astephana* Scort., *Dischidia* sp., and *Hoya* sp., which were rare in the plot, occurred only in association with each other or with other Asclepiadaceae.

Not only the Asclepiadaceae, but the epiphyte flora as a whole was highly gregarious in distribution. The test of gregariousness shows that colonization of rubber trees by an epiphyte species is significantly dependent on colonization by other species ($p<.001$). That is, a tree with an epiphyte species already established is much more likely to be colonized by additional epiphyte species than is an unoccupied tree. This means that in the plantation there are more uncolonized trees than one would expect for random colonization, and the trees which are colonized have more epiphyte species than one would expect.

Because the epiphytic Asclepiadaceae show a highly gregarious distribution, a test for independence of colonization was made with the Asclepiadaceae omitted from the sample. This also shows a non-random ($p<.01$) colonization of the trees by the epiphytes, but the lower statistical significance of this sample indicates that the gregariousness of the asclepiads is a major component of the gregariousness of the epiphyte flora as a whole.

DISCUSSION

The orchids and ferns have minute diaspores which are dispersed as atmospheric dust. All these species, except for one *Dendrobium*, show a

J	J		JNM	X	R			JR				J			AB	AB CJ	ABC JRX	ABC HJ	AC
	K	A	ASP	DF	BL	AL	AC	AH LQ	A				RT		J	JCX	AJ	A	
JKN RU	O		AJO										A				J		
														AM	A	AH IV	AHI JT	AHI LY	AHJ
																		A	AC HQ
J				J		JL			J							J		Q	QRT
J	J	J				J				J					J	J	RH		J
			JT	JT									JT		K			JT	
					R		J	X		JVW	AGW			J	W				
	JR		J	J								JK	DE	X					

Figure 1: Map of epiphytes in a rubber plantation. Each square represents a tree; the letters in a square indicate the presence of those epiphytes in the tree. A square with no letters represents a tree lacking epiphytes.

A. *Dischidia collyris* Wall.
B. *Dischidia rafflesiana* Wall.
C. *Dischidia gaudichaudii* Dcne.
D. *Dischidia* sp.
E. *Dischidia astephana* Scort.
F. *Hoya* sp.
G. *Hydnophytum formicarium* Jack
H. *Myrmecodia tuberosa* Jack
I. *Medinella* sp.
J. *Dendrobium crumenatum* Swartz
K. *Dendrobium secundum* (Blume) Lindl.
L. *Dendrobium* sp.
M. *Calanthe* sp.
N. *Coelogyne* sp.
O. *Bulbophyllum* sp.
P. *Bulbophyllum* sp. 2
Q. *Cymbidium* sp.
R. *Drymoglossum* sp.
S. *Phymatodes sinuosa* (Wall.) J. Sm.
T. *Drynaria* sp.
U. *Davallia* sp.
V. *Platycerium coronarium* (J. König ex O. F. Müll.) Desv.
W. *Lecanopteris carnosa* Blume
X. *Loranthaceae* sp.
Y. *Hippeophyllum celebicum* Schlecht.

random distribution in the sample area. This distribution is consistent with the model of a uniform rain of diaspores arriving from multiple distant sources.

Although ferns were not abundant in the sample plot, they were abundant elsewhere in the plantation. One area in particular was heavily infested with *Platycerium coronarium* (J. König ex. O. F. Müll.) Desv. A few of these were very large plants (to 1.5 m across), and were evidently the original colonists from a distant population, subsequently serving as a source of spores for colonization of neighboring trees, a situation leading to a contagious distribution.

Three of the four fleshy-fruited epiphytes show a random distribution in the plot as would be expected for bird-dispersed species over these distances. *Myrmecodia tuberosa* shows a highly clumped distribution. Janzen (1974) observed that seeds of this species are often dispersed by ants, and Docters van Leeuwen (1929) observed in Java that seeds of *M. echinata* are at least occasionally dispersed by ants, though birds are considered the primary vectors. The occurrence of *Myrmecodia tuberosa* in four adjacent trees, together with ant-inhabited *Dischidia* species in all four trees, suggests that in this case ant-dispersal may be a factor.

Each species of the epiphytic Asclepiadaceae shows a strongly contagious distribution. It seems unlikely that this represents a highly irregular seed rain from a distant source, nor, given the uniformity of the plantation, does it represent differential receptivity of various rubber trees. More probably the clumped distribution of the asclepiads represents rapid colonization of adjacent trees following an initial random establishment in the plantation.

Species of *Dischidia* may spread to adjacent trees by three mechanisms. The species have a creeping habit, attaching to the host tree both by twining and by means of adhesive adventitious roots at the nodes. The creeping and often hanging stems could easily move along the outer branches from one tree to the next, especially along a row where the trees are close together with interpenetrating canopies. In some cases, however, this seems not to have happened where *Dischidia* species on adjacent trees are confined to the trunks and absent from the outer branches. These could be cases of colonization by large, plumose, wind-borne seeds floating to the adjacent tree. Another possibility is that the seeds are transported by ants.

Docters van Leeuwen (1929) observed transport by ants of seeds of *Dischidia rafflesiana* and *D. nummularia* R. Br. in Java. The ants remove the plume from the seed and carry the remaining portion to their nest. The seeds of these species are provided with an oily appendage interpreted by Docters van Leeuwen to be an elaiosome.

Several species of *Dischidia* in this sample are ant-inhabited: *Dischidia collyris* and *D. astephana* harbor ants beneath convex leaves appressed to the tree trunk, while *D. rafflesiana* and *D. sp.* house ants in leaves modified to form globose or flattened hollow pitchers. These are presumed to be mutualistic relationships (Janzen 1974) in which the plants harbor the ants and the ants feed the plants by bringing organic debris and soil into the tree. Most species of *Dischidia* are associated with ants in this way and it would not be surprising if the plants had evolved mechanisms for ant-dispersal of their seeds.

At least three species of ants were common in the rubber trees. One which had nests in the dischidias was a species of *Crematogaster*. A tiny

species of *Monomorium* was common in the trees, but I was unable to determine if it had nests in the epiphytes. The ants were found predominantly in the trees containing epiphytes, but were also present in other trees.

Not only do the epiphytic species of Asclepiadaceae in the plot have contiguous distributions, but they are highly gregarious as well, a situation I have noticed elsewhere in Malaysia and Thailand. Two or more species of *Dischidia* and/or *Hoya* are more likely to be found in a tree than just one. In part this reflects a very uniform habitat preference among the species of these genera. It also reflects the likely outcome of a situation where ants are scavenging asclepiad seeds and carrying them to their nests.

The demonstrated gregariousness of the epiphyte flora as a whole in this sample may also be related to the activities of ants. Thirteen of the 25 epiphyte species in this sample are ant-associated (the Asclepiadaceae; *Hydnophytum*, *Myrmecodia*, *Phymatodes*, *Lecanopteris*, and *Bulbophyllum* all with hollow, ant-inhabited stems; and *Platycerium* and *Drynaria* with ants nesting between the appressed sterile leaves and the tree trunks). The gregariousness of ant-epiphytes was first mentioned by Ule (1901, 1906) in his descriptions of 'ant-gardens' in South America. Janzen (1974) has noted a similar situation in white sand savannas in Sarawak at Bako. Ant-gardens I have observed in the Andes also normally include several species of epiphytes, usually with *Anthurium*, *Peperomia*, and *Codonanthe* predominating.

The regular occurrence of several species of epiphytes in a clump may reflect the scavenging of epiphyte seeds by ants, as suggested by Ule (1906), Docters van Leeuwen (1929) and Janzen (1974). Alternatively, ant nests or pioneer species of epiphytes may provide sites especially suitable for germination of seeds of other epiphytes, so that the observed epiphyte communities are the result of an ecological succession. This situation has been demonstrated in West Africa by Johansson (1974), without implicating the activities of ants. Went (1940) suggested that accumulation of humus by one or more pioneer species may have been the basis of epiphyte communities he observed in Java. The processes resulting in the gregarious distribution of the epiphytes in this study cannot be determined from the data at hand, but activities of ants and ecological succession may both be involved.

SUMMARY

The distribution of vascular epiphytes in a rubber plantation in Sarawak was investigated. Species with minute diaspores dispersed as atmospheric dust, and fleshy-fruited species dispersed by birds showed a random distribution in the plantation. Species of epiphytic Asclepiadaceae showed a highly contagious distribution interpreted as the result of spread to neighboring trees by originally randomly distributed colonists. The epiphyte flora as a whole is highly gregarious, a situation in which the activities of ants are implicated.

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